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Opinion

Parasitism as a Driver of Trophic Niche Specialisation

J. Robert Britton[1,*] and Demetra Andreou[1]

The population trophic niche of free-living species can be subdivided into smaller niches comprising individuals specialising on specific food items. The roles of parasites in creating these specialised subgroups remain unclear. Intrapopulation differences in parasite infections can develop from specialist individuals within populations. Their differences in morphology and habitat can increase their exposure to intermediate hosts via infected prey, altering their parasite fauna. However, we also suggest that parasite infections can drive this niche specialisation. Through mechanisms including parasite manipulation, altered host phenotypes, and/ or parasite-mediated competition, parasites can alter the resource availability of their hosts, altering their trophic niches. Thus, trophic niche specialisations could result from parasitism via varying influences on host traits, raising questions for future research.

Individual Trophic Niche Specialisation in Free-Living Species

The trophic niche of a population describes the extent of the food resources it exploits. It can comprise a series of subgroups of smaller niches formed by individuals that specialise on specific food items [1–3]. These subgroups might be focussed on consuming specific prey items that are also being consumed by their more generalist conspecifics, such as larger salmonid fish in forest streams that feed more on terrestrial insects compared with smaller conspecifics [4]. This represents **trophic niche constriction** (see Glossary), with the size of the population trophic niche remaining unaltered. Conversely, the specialist individuals might be exploiting alternative resources; for example, where larger brown trout *Salmo trutta* in lentic environments switch from insectivory to piscivory [5]. This results in **trophic niche divergence** and increases the population niche size [4,5] (Figure 1). Identified drivers of **individual trophic niche specialisation** include changes in the strength of inter- and intraspecific competitive interactions (e.g., following the introduction of a new free-living species [6]), the exploitation of new ecological opportunities (e.g., the seasonal exploitation of terrestrial insects by stream fish [4]), and the direct and indirect consequences of predation pressure that alter predator–prey relations [7,8]. Despite this extant knowledge of the ecological drivers of niche specialisation, there has been little consideration of how natural enemies, such as parasitoids, parasites, or pathogens, influence its development and subsequent magnitude [8].

Individual Trophic Niche Specialisation and Parasites

We suggest that there are two primary aspects to the role of parasites in trophic niche specialisation. First, infections by specific parasites can be a consequence of trophic niche specialisation. For example, where there are intrapopulation differences in body and **functional morphology**, and habitat and resource utilisation, individuals will be differentially exposed to prey populations that comprise **intermediate hosts** of specific parasites, as observed in polymorphic Arctic charr (*Salvelinus alpinus*) populations [9]. Second, infections by specific parasites can drive trophic niche specialisation [10], such as via **parasite-mediated competition** [11,12]. This is where alterations to the host phenotype can affect their interactions with their prey communities, uninfected

Trends

Populations of generalist free-living species are increasingly shown to comprise small subsets of relatively specialised individuals, including those in their trophic niches.

Recent studies indicate that drivers of intrapopulation trophic niche specialisation include shifts in competitive interactions and predation pressure, but the potential roles of parasites have not been quantified.

Heterogeneous phenotypic traits in individuals across a population can result in contrasting parasite infections due to variation in exposure to intermediate hosts.

Parasite-induced trophic niche specialisation could develop in populations comprising host and uninfected conspecifics via altered phenotypic traits from manipulative and non-manipulative parasites.

The altered phenotypes would drive trophic niche specialisation through their alteration of prey availability and host selectivity.

[1]Department of Life and Environmental Sciences, Faculty of Science and Technology, Bournemouth University, Fern Barrow, Poole, Dorset, UK

*Correspondence: rbritton@bournemouth.ac.uk (J.R. Britton).

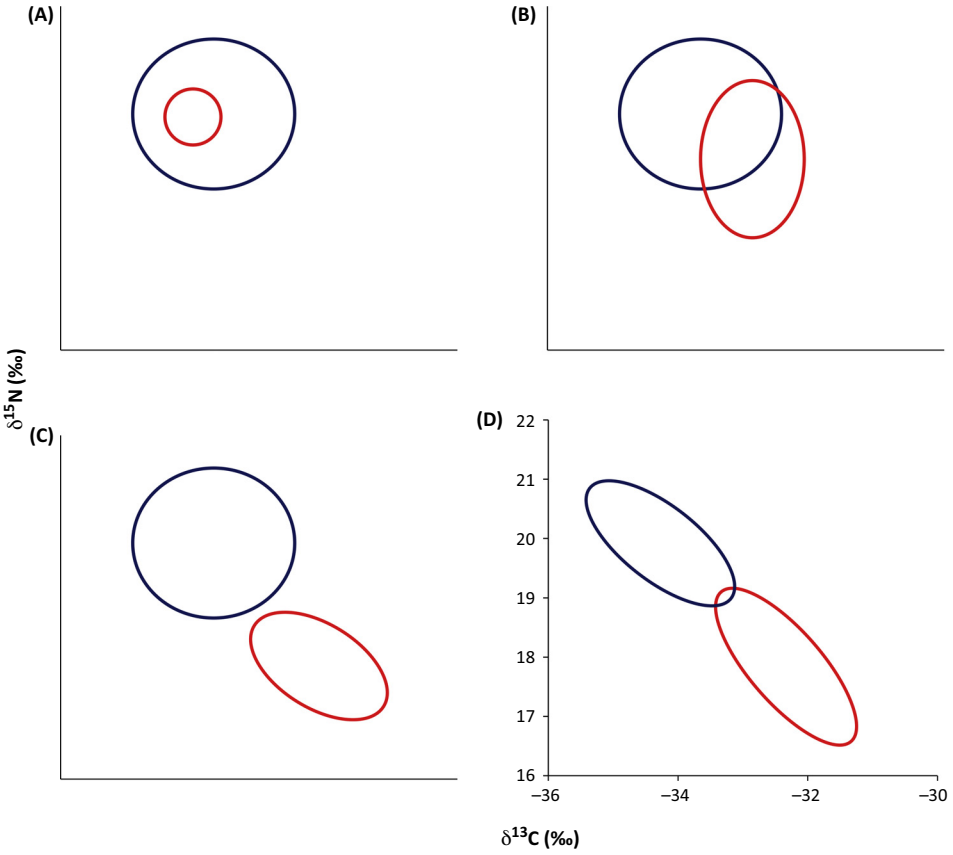

Figure 1. Representations of the Trophic Niches of Infected and Uninfected Conspecifics of a Parasitised Population. (A) Niche constriction. The infected niche (red) is within that of uninfected (blue) conspecifics, indicating infected host specialisation on specific items already present in the diet of the population. (B) Partial trophic niche divergence. The infected (red) niche has some overlap with uninfected (blue) conspecifics, but indicates some exploitation of alternative resources. (C) Complete trophic niche divergence. The infected (red) niche has no overlap with uninfected (blue) conspecifics, indicating exploitation of alternative resources. (D) The trophic niche breadths of *Cyprinus carpio* that are uninfected (blue) and infected (red) with the tapeworm *Bothriocephalus acheilognathi* in a pond in southern England in October 2013, indicating almost complete niche divergence between the population subgroups. In (D), the trophic niche sizes were calculated as standard ellipse areas (SEAc) [62] using *C. carpio* stable isotope data (δ^{13}C and δ^{15}N) [10]. Adapted from [10] (D).

conspecifics, and nonhost species, altering their diet composition and trophic niche [12] (Table 1). For example, studies suggest that infections of the intestinal parasite *Strongyloides robustus* are at least partially responsible for altering the competitive interactions between two species of flying squirrel from the genus *Glaucomys* in the eastern USA [13].

In this opinion article, we explore these two aspects to identify the potential ecological roles and evolutionary significance of parasites in the trophic niche specialisation of their free-living hosts (Table 1). Outstanding research questions are highlighted that will enable relevant hypotheses to be derived and tested, and more integrative approaches to be developed. Note that vertebrates, especially freshwater fish, dominate the literature on trophic niche specialisation (e.g., [1,2,8]) and this will be generally reflected in our examples. Matthews *et al.* [14] suggested that niche specialisation is most common in upper **trophic levels**, while Svanbäck *et al.* [15] suggested the highest among-diet variation in Eurasian perch (*Perca fluviatilis*) was at intermediate trophic positions. This means that our examples are often focussed at these intermediate and higher

Glossary

Complex lifecycle: the lifecycle of a parasite that involves more than one host stage, such as an intermediate and final host stage

Food web: a representation of the feeding interactions of species in an ecosystem that are connected by pairwise interactions.

Functional morphology: the morphological adaptation of an individual to a specialist function, such as feeding.

Fundamental trophic niche: the potential extent of the trophic niche of a population as determined from abiotic factors and independent biotic factors, such as competitive pressures.

Individual trophic niche specialisation: where the population trophic niche consists of subgroups of trophically specialised individuals that in entirety comprise the population niche.

Intermediate host: a host of a parasite with a complex lifecycle that is important for an aspect of its development but in which sexual maturity does not occur.

Manipulative parasite: a parasite that alters aspects of the phenotypic traits and behaviours of its hosts, such as their morphology, foraging behaviour, and habitat use, which either increases the probability of their transmission from one host to another and/or ensures that their propagules are released in an appropriate location.

Non-manipulative parasite: a parasite whose infection alters aspects of the phenotypic traits and behaviours of their hosts, such as their morphology, foraging behaviour, and habitat use, due to, for example, pathological impacts and energetic costs, and is not associated with the parasite manipulating the host to increase its probability of transmission.

Parasite-increased trophic transmission: transmission of the parasite from an intermediate stage to the next stage occurs via predation.

Parasite-mediated competition: infection alters the competitive dynamics between interacting species via density and trait effects. Where the otherwise superior competitor species is heavily influenced by the parasite, the

Table 1. Processes, Mechanisms, and Influences of Parasites on Free-Living Species that Could Affect the Trophic Niche Specialisation of Hosts

	Influence on Hosts	Potential Outcome for Trophic Niche Specialisation	Refs
Ecological drivers of trophic niche specialisation	Heterogeneity in the morphology and behaviour of individuals within populations of free-living species results in their spatial segregation and trophic niche specialisation, irrespective of parasites	Populations comprise subgroups of individuals with contrasting parasite communities through their differing exposure to intermediate hosts	[9]
Parasite-mediated competition	Sublethal infection consequences affects competitive abilities of hosts, resulting in increased asymmetry in their intra- and interspecific competitive interactions	Hosts exploit alternative prey resources (niche divergence from conspecifics) or increasingly specialise in extant resources (niche constriction)	[11,12]
Manipulative parasitism	Manipulated behaviours of hosts influence their prey availability and accessibility as infection alters their behaviours via parasite-increased trophic transmission	Spatial and prey resource segregation of infected and uninfected conspecifics results in their trophic niche divergence.	[35–41]
Parasite-modified phenotype	Host functional traits are impaired through sublethal impacts of infection, altering their prey selectivity, irrespective of competitive pressures	Hosts increasingly focus on specific dietary items (niche constriction) or new resources (niche divergence)	[10,26]
Novel trophic links	Infection results in impaired functional traits and/or modified behaviour of hosts that provides a novel prey opportunity for nonhost species to exploit	Nonhost species exploit a novel prey item, potentially resulting in a shift or specialism in their trophic niche	[55]
Overdispersal of parasite	Abundance of the focal parasite is only relatively high in a low proportion of the host population	Host phenotypic modifications are limited to a few individuals with minimal influence on the population trophic niche	[58]
Parasite spillover	A parasite introduced with a free-living species is transmitted to a native species through host switching, potentially resulting in modified traits and behavioural shifts	New hosts exploit alternative prey resources (niche divergence) or increasingly specialise in extant resources (niche constriction).	[58]
Parasite spillback	An introduced free-living species becomes either a competent host of native parasites that acts as either an infection reservoir for native host species or an incompetent host acting as an infection sink	Temporal changes in parasite prevalence and abundance in host populations, resulting in temporal shifts in their trophic niche according to the variability in infection consequences	[58]
Reciprocal effects between host and parasite	Current infections may increase host vulnerability to new infections	New infections increase the extent of modifications to the host phenotype, potentially exacerbating current niche divergence/constriction patterns	[56,57]
Habitat homogeneity	Disturbed environmental conditions results in homogeneity in habitat and prey resources for host and uninfected conspecifics	Intrapopulation spatial and resource segregation is limited, resulting in homogeneity in trophic niche of infected and uninfected conspecifics, irrespective of parasite burdens	n/a

trophic levels. However, we suggest that the paradigms and principles described will have applicability across aquatic and terrestrial ecosystems, and over a range of animal and parasite taxa. Our focus is also primarily on the effects of macroparasites, especially those with **complex lifecycles** involving intermediate hosts. Where the terms 'infected' and 'uninfected' are used,

process is likely to favour co-existence.

Population trophic niche: extent of the food resources exploited by a population as set by abiotic and biotic constraints.

Realised trophic niche: the actual trophic niche of a population that is smaller than its fundamental niche due to the limiting pressures of biotic factors, such as competition.

Red Queen dynamics: the abundance of host species and their parasites exhibit alternating dominance (such as year-to-year) to provide population sustainability and maintain fitness.

Trophic level: the feeding positions within a food chain, such as primary producer, primary consumer, and secondary consumer, where a food chain represents a succession of species that consume the one(s) before them in the chain.

Trophic niche constriction: individuals in the population subgroup consume a restricted range of food items that are also present in the diet of more generalist conspecifics.

Trophic niche divergence: individuals in the population subgroup consume different food items that are not present in the diet of their conspecifics.

Trophic vacuum: the difference in trophic levels between free-living propagules of a parasite and its final host that, for trophically transmitted parasites, is overcome by use of intermediate hosts within their lifecycle.

they refer to the infection status of an individual in relation to a particular parasite. We also primarily refer to specialisations in the **realised trophic niches** of populations, rather than their **fundamental trophic niche**.

Parasite Infections and Trophic Niche Variation

Contrasting parasite infections can develop between individuals in a population as a consequence of existing trophic niche specialisations. These specialisations result from intrapopulation variability in the morphology (e.g., body and gape size), habitat utilisation (e.g., littoral versus open water), and foraging behaviours (e.g., time spent foraging) of individuals [16–20]. Traits that enable specialised feeding behaviours to develop in individuals can elevate their exposure to intermediate hosts of trophically transmitted parasites [2]. For example, the interactions of habitat use, morphology, and diet composition of individual *S. alpinus* strongly influence their parasite infections, resulting in subgroups of fish with homogenous traits, dietary specialisms, and parasite infections that differ significantly with other subgroups [1,21–24]. In European eel *Anguilla anguilla*, individuals with broader heads tend to be more piscivorous, because this increases their gape size [25]. This difference in functional morphology leads to these specialist individuals having increased probabilities of infection by the non-native nematode parasite *Anguillicoides crassus* due to its transmission via paratenic fish hosts [26], a common mode of transmission in this host–parasite system [27].

Of arguably greater ecological and evolutionary significance is how parasitism can be the driver of trophic niche specialisation. This is because infections by certain parasites are known to have considerable consequences for their free-living hosts, including alterations in habitat utilisation, foraging, and antipredator behaviours [28–31]. These parasites can be grouped into **manipulative parasites**, which alter the behaviour of their intermediate hosts to facilitate transmission to the next host, and **non-manipulative parasites**, which can affect the trophic niche of infected individuals via their impairment of host phenotypic traits, which is independent of manipulation.

Host manipulation can assist parasites to fill the **trophic vacuum**. This is the distance between the trophic levels of, for example, the parasite propagules of low trophic levels and their final hosts at much higher trophic levels [32,33]. Parasites have evolved complex lifecycles to overcome this vacuum, using intermediate hosts to navigate through the trophic levels, with their manipulation of host behaviours increasing transmission rates. This aligns to the **parasite-increased trophic transmission hypothesis,** where the manipulation of intermediate host behaviours increases their probability of predation by the next host (Table 1) [17]. In combination, this suggests that the strongest effects of manipulation on trophic niche specialisation will be in species at intermediate trophic levels.

Amphipods provide strong examples of intermediate hosts that are manipulated by their parasites to facilitate their predation by a fish or bird final host. For example, when *Gammarus roeseli* are infected with *Polymorphus minutus*, they exhibit reverse geotaxis [34]. This substantially lengthens the time they spend at the water surface, increasing their predation risk by avian final hosts; it is also far from their usual benthic food resources [35,36]. Consequently, infected individuals consume less epilithon than uninfected individuals, but more of the terrestrial detritus that is encountered at the water surface [37], thus forming a population subgroup with a diverged trophic niche that in turn increases the population trophic niche size. Populations of *Gammarus insensibilis* are parasitically subdivided into two groups by the trematode *Microphallus papillorobustus* [38]. Infected individuals inhabit the surface of salt marshes and uninfected conspecifics remain near the bottom [38]. This shift in habitat use again favours the predation of hosts by bird final hosts and has similarly strong implications for the trophic niche of the infected (pelagic) and uninfected (benthic) subgroups, and, thus, the population trophic

niche. Parasite manipulation has also been detected in fish intermediate hosts, with the cestode parasite *Ligula intestinalis* generally recognised as modifying the behaviour of its intermediate fish hosts. Infected fish increasingly utilise habitats, such as the littoral zone, that increase their predation by their definite host, a piscivorous bird [39,40]. These habitat shifts alter their access to food resources with, for example, infected roach *Rutilus rutilus* in a reservoir in the Czech Republic consuming fewer food items and ingesting less food than uninfected conspecifics, but consuming more animal material [41], representing a substantial shift in their niche.

Parasite infections can also result in substantial modifications of the host phenotype that is independent of manipulation. These include impaired traits and altered behaviours [22], which can influence prey selectivity [10]. For example, common carp *Cyprinus carpio* is a final host of the non-native intestinal cestode parasite *Bothriocephalus acheilognathi*, with infections impairing the foraging ability of hosts [42–44]. This results in infected individuals increasingly specialising on less-motile food sources, resulting in a larger population trophic niche that is divided into infected and uninfected subgroups [10] (Figure 1). Moreover, the infected subgroup consuming alternative resources is likely to be exposed to new competitive and predatory pressures that arise from its novel trophic interactions; these could further modify its niche and concomitantly create new links within the food web [31].

The phenotypic modification of infected individuals results in these traits having a bi- or multimodal distribution in the population, resulting in distinct population subgroups in which individuals are grouped by their homogenous traits [45]. Where these traits affect their habitat utilisation, foraging behaviours, and competitive abilities (Table 1), they will affect the prey selectivity and predation abilities of individuals [10]. This was demonstrated in another amphipod species, *Gammarus pulex*, when feeding on the isopod *Asellus aquaticus*. Individuals infected by the acanthocephalan *Echinorhyncus truttae* killed significantly fewer *A. aquaticus* than their uninfected conspecifics, with a tendency to only kill the smaller size classes [46]. Although this specialisation might not necessarily affect the size of the population trophic niche, it could result in infected individuals also predating more on alternative species, resulting in some niche divergence. This selective removal of smaller prey size classes could also then impact the population growth of *A. aquaticus*, resulting in further food web perturbations.

Parasite infections can also alter host foraging-time budgets and associated prey selectivity, with three-spined sticklebacks *Gasterosteus aculeatus* infected with *Schistocephalus solidus* increasing their time spent foraging at the expense of antipredator behaviour [47], and selecting smaller prey items compared with their uninfected conspecifics [48,49]. Conversely, Ranta *et al.* [50] suggested infected individuals selectively preyed on larger items than uninfected conspecifics and this compensated for the energy costs of infection. Irrespective of these different outcomes, these studies demonstrate that infections caused shifts in the prey selectivity of hosts that could then influence their trophic niches and the size structure of the prey population.

The modification of the host phenotype can also depend on the consequences of specific parasite infections, with different parasites potentially causing contrasting outcomes for host habitat utilisation and, thus, access to food resources. In intertidal snail populations, infections by different larval trematode parasites have distinct effects on host habitat utilisation. For example, in *Batillaria attramentaria*, infections of *Cercaria batillariae* result in hosts having abnormally large shells and they inhabit the lower areas of the intertidal zone [19,51]. When infected with renicolid cercariae, the increase in host shell size is small and they inhabit the upper areas of the intertidal zone. However, when infected by both parasites, hosts have an intermediate shell size and inhabit the areas between the two extremes [19,51]. Thus, the host population becomes parasitically divided, resulting in three subgroups of contrasting habitat utilisation that affects resource access, thus potentially impacts their trophic niche.

Finally, the parasite fauna of animal communities can also be impacted by anthropogenic disturbances. Activities, such as fishing, that selectively harvest species in specific size classes can decrease the abundance of trophically transmitted parasites in the exploited species, as observed in the fish communities of the Line Islands in the equatorial Pacific [52]. The interaction between fishing, compensatory responses in surviving fish, and parasite diversity can then further modify the host phenotypes and their exposure to intermediate hosts [52], and so have implications for the development of specialisations within the population trophic niche.

Parasite-Mediated Trophic Niche Shifts in Nonhost Species

The novel trophic interactions that can develop as a result of parasite-mediated effects could also affect the trophic niche of nonhost species in the community that are otherwise unaffected by the parasite [11] (Table 1). For instance, infections can substantially increase the accessibility to prey populations that would otherwise be difficult to capture. Examples include cockles with heavy trematode infections in their foot that prevents them from burying into mudflats, thus creating a new feeding opportunity for a range of fish and birds, potentially diverging the trophic niches of their populations [53]. Infections by acanthocephalan parasites in *G. pulex* can increase their vulnerability to predation by a range of invertebrate species, despite these predators not acting as hosts [54]. Parasite infections can also result in new feeding opportunities through the creation of novel nutrient transfer between ecosystems, such as between terrestrial and freshwater systems. Examples include fish of the Salmonidae family predating on crickets and grasshoppers (e.g., *Nemobius sylvestris*), which act as novel dietary items when they are parasitised by hairworm parasites (e.g., *Paragordius tricuspidatus*). Their manipulation results in hosts jumping into the water; the parasite completes its lifecycle, while the fish are presented with a novel feeding opportunity that should increase the extent of their trophic niche [55].

Effects of Multiple Parasite Infections

Given that individuals are often infected by multiple parasites, the potential impact of co-infections on the trophic niche must also be considered. Deciphering the influence of infections by multiple parasites species can be challenging, because their effects could be synergistic, antagonistic, or neutral [28]. Synergistic effects can lead to 'vicious circles' of infection, where, following transmission of a new parasite, hosts are increasingly vulnerable to subsequent infections [56,57] (Table 1). This could then lead to further modification of the host phenotype, a potentially stronger shift in their foraging behaviours, and, thus, trophic niche specialisation [58]. However, it could also result in greater energetic costs and, ultimately, the death of the host [59]. In the case of B. *attramentaria* infected with both *C. batillariae* and renicolid cercariae, antagonistic interactions between the parasites were suggested because they appeared to compete for successful transmission to the final host, resulting in only moderate alterations of host phenotypes compared with the more extreme alterations detected with single infections [19,51]. In *G. aculeatus*, controlled co-infections at different levels of infectiveness of the manipulative parasites *S. solidus* and *Camallanus lacustris* had substantial impacts on parasite manipulation with, for example, infective *S. solidus* suppressing the manipulation caused by a not-yet infective *C. lacustris* [60]. Given that parasite manipulation is a potentially key process for driving trophic niche specialisations, the effects of these co-infections could have important implications for its development.

Concluding Remarks

Future research can initially focus on empirically answering relevant questions (see 'Outstanding Questions') and testing their associated hypotheses on the potential shifts that occur in the foraging behaviours and trophic ecology of hosts following parasite infections. Outputs can quantify the parasite-driven processes and mechanisms that result in the development of trophic niche specialisations between infected and uninfected population subgroups (Table 1).

Outstanding Questions

Can trophic niche specialisations caused by parasite manipulation be decoupled from those caused by infection-driven modifications of host phenotypic traits?

What is the importance for population trophic niches when trophically transmitted parasites use free-living species as intermediate hosts to overcome the trophic vacuum?

How do temporal changes in parasite prevalence (due to **Red Queen dynamics**) affect the trophic niche of the final host population and what is the resulting influence on the population dynamics of intermediate hosts?

Does parasite-mediated competition lead to trophic niche specialisation between infected and uninfected conspecifics? How does this affect their trophic interactions with nonhost species?

How does parasite-driven trophic niche specialisation influence the fitness of infected and uninfected conspecifics and what are the selection implications?

When new species and their associated parasites are introduced in new communities, what are the consequences for the trophic niches of extant species and food web structure?

What is the ecological significance of short-term trophic links created by heavily infected hosts before their mortality?

What is the influence of parasite aggregation on the phenotypic traits and trophic niche of infected hosts?

What are the consequences of varying parasite infection levels on trophic niche specialisation at the individual and population level?

How do multiple parasite infections influence trophic niches at the individual and population level?

Approaches should focus on decoupling the ecological drivers of parasite infections from their ecological consequences. The role of parasite-mediated competition in driving the trophic niche specialisation of hosts is also important, particularly in relation to the novel trophic links that this can result in in the food web. These include the creation of new competitive interactions with nonhost species, and the extent to which this alters energy flux in the food web. Evolutionary perspectives may be informed by whether the interactions of parasitism and trophic niche specialisations affect the fitness of individuals through additive or synergistic effects, and so can identify the implications for selection (see Outstanding Questions).

Analytical approaches to quantify the role of parasites in trophic niche specialisations can integrate the qualitative food web approaches that have dominated parasite food web research [45,52] with stable isotope analyses that reveal more quantitative perspectives [58], such as the trophic consequences of infections according to parasite burdens [43] and the parasite-mediated modifications to energy flow between trophic levels [58]. Relatively recent developments in quantitative stable isotope metrics enable estimates of trophic niche breadth to be calculated, often from relatively small sample sizes [61,62]. These comparisons of the trophic niche size of the infected and uninfected components of parasitised populations enable their assessment in respect of parasite-induced trophic niche constriction and divergence [10] (Figure 1; Table 1). Integrated field and experimental approaches will then be important in developing the underlying ecological and evolutionary theory that bridges the fields of trophic and food web ecology with parasitology. Finally, we suggest that, because the emphasis here has been on species within aquatic systems using macroinvertebrate- and fish-based examples, there is a need to determine whether the patterns and research questions have more general applicability across a wider range of taxa and systems.

Thus, the realised trophic niches of populations of generalist free-living species are increasingly recognised as comprising small subgroups of relatively specialised individuals [1–3], with the drivers of these trophic specialisations including competitive interactions and predation pressure [8]. Here, we have argued that parasite infections can also strongly influence population trophic niches due to the infection consequences of manipulative and non-manipulative parasites that strongly influence host phenotypic traits (Table 1). We suggest that processes such as parasite-mediated competition have large implications for intrapopulation trophic niche specialisation, as well as other aspects of food web structure [11,12].

In closing, we emphasise that, in assessing the ecological significance of intrapopulation trophic niche specialisation, there is a compelling requirement for a greater emphasis on the role of natural enemies, especially parasites. This suggests that further empirical and theoretical research is required to decouple the effects of parasitism on trophic niche specialisation from those of other ecological interactions, with our 'Outstanding Questions' providing the basis for such research.

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